NEW TAXA OF *CALADIUM*, *CHLOROSPATHA*, AND *XANTHOSOMA* (ARACEAE: COLOCASIOIDEAE) FROM SOUTHERN CENTRAL AMERICA AND NORTHWESTERN COLOMBIA[1]

MICHAEL H. GRAYUM[2]

ABSTRACT

Six new infrageneric taxa of Araceae, subfamily Colocasioideae, are described. *Chlorospatha hammeliana* is described from a restricted area of Panama, *C. croatiana* ssp. *croatiana* from Costa Rica and Panama, and *Caladium lindenii* (André) Madison var. *sylvestre* from Panama and Colombia. These represent the first reported indigenous occurrences of the genera *Caladium* and *Chlorospatha* outside of South America. In addition, *Chlorospatha gentryi* and *C. croatiana* ssp. *enneaphylla* are described from northwestern Colombia. *Chlorospatha croatiana* and *C. gentryi* are the fourth and fifth species of their genus known to have compound leaves; a key is provided to all five. A brief review of generic distinctions within the tribe Caladieae precedes the description of the second known peltate-leaved species of *Xanthosoma, X. caladioides,* from eastern Panama.

The tribe Caladieae (sensu Madison, 1981), belonging to the subfamily Colocasioideae of the overwhelmingly tropical family Araceae, consists of six genera and 70–75 species, all confined to the New World. Three of the genera, *Aphyllarum, Jasarum,* and *Scaphispatha,* are monotypic and of restricted distribution in South America and will not be considered further in this paper. The remaining three genera, *Caladium, Chlorospatha,* and *Xanthosoma,* comprise the bulk of the species and range more widely, though only *Xanthosoma* has been heretofore reported to extend beyond South America (Croat, 1979; Madison, 1981).

The Caladieae appear to be especially diverse in the Andean regions of northern South America, and recent work on newly available collections from that area (Madison, 1981) has led to the clarification of generic concepts in the group. These refined concepts have, in turn, facilitated the placement of new taxa collected in South America and other regions, including those described below.

CALADIUM

Caladium lindenii (André) Madison is well known in cultivation as an ornamental plant with whitish or silvery leaf venation. This species is more commonly, but improperly, known as *Xanthosoma lindenii* (André) Engl., the transfer to *Caladium* having been made only recently (Madison, 1981). It was first described, as *Phyllotaenium lindenii* André, in 1872, from plants supposedly collected in Colombia; although persisting in cultivation, the species was not found again in the wild until 1939, when a form with plain green leaves was collected in Chocó Department, Colombia (*Killip 35140,* COL). Subsequent collections have extended the known natural range of this species—and consequently of the genus *Caladium*—into central Panama. All collections of the plain-leaved form have, until recently, either been misidentified or left undetermined.

The "wild type," plain green-leaved form of *Caladium lindenii* is described below as a new variety.

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[1] I am grateful to Thomas B. Croat for assistance in my work at the Missouri Botanical Garden and for providing the photographs of *Chlorospatha croatiana* and *C. hammeliana.* I also thank Alwyn H. Gentry for allowing me to use his photo of *C. gentryi.* Barry E. Hammel supplied fresh pollen samples from the field, in addition to herbarium specimens, and Frances Mazanec critically reviewed and rewrote the Latin diagnoses for all taxa except *Xanthosoma caladioides*; to both of these individuals I am deeply appreciative. The investigation of pollen morphology in *Caladium lindenii, Chlorospatha croatiana,* and *Chlorospatha hammeliana* was facilitated by National Science Foundation grants to James W. Walker as well as an Albert DeLisle Scholarship (University of Massachusetts) to the author.

[2] Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166.

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Caladium lindenii (André) Madison var. **sylvestre** Grayum, var. nov. TYPE: Panama. Panamá: El Llano–Cartí Rd., 9 mi. from turnoff of PanAmerican Hwy., ca. 300 m, *Hammel et al. 11341* (holotype, MO-2982267).

Var. *sylvestre* typico immaculatis viridis laminis distinguenda. Lamina simplex, sagittata, inferiore pagina minute ferrugineo-furfuracea; petiolus 40–95 cm longus, ferrugineo-furfuraceus; lobus anticus 25–35 cm longus, 15–25 cm latus; lobus posticus 9–18 cm longus. Inflorescentia solitaria; pedunculus 6–17 cm longus; spatha 8–12 cm longa; tubus 4–5 cm longus; spathae lamina 5–8 cm longa; spadix pars mascula 4–4.5 cm longa.

Terrestrial herb, ca. 75 cm tall. Stem ca. 2–2.5 cm diam. (*Croat 52023, 56094*), largely or entirely subterranean. Petiole purplish at the base, "narrowly flattened" (*Croat & Cagallo 52150*) to "narrowly and obtusely sulcate" (*Croat 56094*) adaxially, with scant milky sap or sap not evident at all, 40–95 cm long, covered with sparse, tangled, reddish brown scurf. Lamina sagittate, not peltate, the anterior lobe 25–35 cm long, 15–25 cm broad, the posterior lobes 9–18 cm long (measured along main vein). Leaves uniformly green on both surfaces (midrib and proximal parts of major veins white in *Croat 52023*), matte and dark green above, much paler below and minutely covered with reddish brown scurf; major veins sunken above, the smaller veins conspicuous beneath, darker than the lamina. Inflorescence solitary (or perhaps occasionally paired), peduncle 6–17 cm long. Spathe 8–12 cm long; tube green to purplish, 4–5 cm long; blade white, 5–8 cm long. Spadix ca. 7.5–9.5 cm long; female part of spadix ca. 1.5–2.5 cm long; sterile part 1.5–2.5 cm long; male part 4–4.5 cm long, white. Pollen in monads, inaperturate, subspheroidal, perfectly psilate, 34–43 μm (mean 38 μm) diam., starch-bearing, trinucleate.

Distribution. *Caladium lindenii* var. *sylvestre* is currently known from the departments of Antioquia and Chocó, Colombia, and the Province of Panamá, Panama. It has been collected mostly in deep, shaded primary forest, on slopes near creeks, from near sea level to about 600 m; the label on *Denslow 2672* reads "common in second growth."

The population of *Caladium lindenii* recently discovered along the El Llano–Cartí Rd. in central Panama represents the first known indigenous occurrence of this genus outside the South American continent (see Croat, 1979; Madison, 1981).

The seven flowering collections were made in February, March, April, August, and October.

The vulgar name "picha de gato" is recorded on the label of *Folsom et al. 5785.*

Caladium lindenii var. *sylvestre* differs from the "typical" var. *lindenii* in its plain green, unvariegated leaves. According to the description of *C. lindenii* provided by Madison (1981), var. *sylvestre* would also appear to differ in having considerably larger overall dimensions—especially with regard to leaf measurements, petiole length, peduncle length, spathe length, and the length of the male portion of the spadix. In all of these categories, the ranges of measurements for the two varieties overlap scarcely if at all. That the two forms are nonetheless conspecific is indicated by their distinctive sagittate leaf shape and tangled, reddish brown, scurfy indumentum, as well as by the tendency toward whitening of the major veins seen in one collection of var. *sylvestre.* In any case, the purported size difference is spurious, since many specimens of var. *lindenii* (e.g., *Hutchison 8456,* MO) are every bit as large in all respects as var. *sylvestre.* Madison's measurements must have been taken from a poorly grown specimen, or a particularly small cultivar.

The rediscovery of *Caladium lindenii* in the wild as a plain green-leaved form suggests the possibility that other rare aroid species currently known only from variegated specimens (e.g., *Zomicarpella maculata* N. E. Br.) may also prove to have predominantly concolorous foliage in the wild state. Horticulturists have long favored oddities such as variegated foliage, and it is not unreasonable to suggest that collectors in search of ornamental subjects might have bypassed whole populations of plain green-leaved individuals, pausing only to dig up the occasional attractive, yet anomalous specimen—which, when shipped back to Europe, may well have come to "typify" certain species. This is clearly what must have happened in the case of *Caladium lindenii* and is also suspected in other aroid species such as the familiar "pothos" of horticulture, which is unknown in the wild state. Known variously as *Scindapsus aureus* Engl., *Rhaphidophora aurea* (Engl.) Birdsey and, most recently, *Epipremnum aureum* (Engl.) Bunting, it is now believed to represent nothing more than a variegated form of the widespread Asian species *E. pinnatum* (L.) Engl. (Nicolson, 1978).

Specimens examined. COLOMBIA. ANTIOQUIA: municipio of Anorí, *Soejarto et al. 3197* (MO); Río Anorí valley, *Shepherd 533, 647* (WIS), *Denslow 2672* (WIS); between San Luis and Puerto Triunfo, *Croat 52023* (MO). CHOCÓ: between Quibdó and Istmina, *Croat & Cagallo 52150* (MO); near Río Iró, S of Istmina, *Croat 57398* (MO); region of Río Baudó, *Fuchs 22269* (COL); Serranía de Baudó, between Las Animas and Pato, *Croat 56094* (MO).

PANAMA. PANAMÁ: El Llano–Cartí Rd., *Folsom et al. 5785* (MO), *Hammel et al. 11341* (MO), *Hammel & Kress 13392* (DUKE).

CHLOROSPATHA

The genus *Chlorospatha,* regarded for nearly a century as monotypic, owes its present status as a moderately sizable genus to Madison's (1981) realization that *C. kolbii* Engl., the original species, differed from several species then constituting the genus *Caladiopsis* only in its possession of compound leaves. This being a character of no significance at the generic level among New World Colocasioideae, the two genera were combined under the older name.

As indicated previously, the genus *Chlorospatha* has never before been reported from outside the South American continent. Plants belonging to this taxon have, in fact, frequently been collected from Panama over the past decade; the specimens, however, have generally been misfiled with the more familiar genus *Xanthosoma.* The two genera may be easily distinguished on the basis of vegetative (*Xanthosoma* is frequently cormose; *Chlorospatha* never is) and floral characters (*Chlorospatha* has more slender and elongate inflorescences on more delicate peduncles, with the female portion of the spadix usually at least partly adnate to the spathe). For further details, the reader is referred to the important paper of Madison (1981).

Chlorospatha and *Xanthosoma* are also palynologically distinct; indeed, the first indication that the two mainly Panamanian species described below were members of the genus *Chlorospatha* was provided by an examination of fresh pollen, without recourse to sporophytic material. The two genera are unique in Araceae in shedding pollen in permanent tetrads; as Madison (1981) has indicated, the individual grains (as well as the tetrads) of *Chlorospatha* average considerably smaller than those of *Xanthosoma*—more than 50% smaller, in fact (Grayum, 1984). In addition, pollen of *Chlorospatha* lacks starch and is basically binucleate, whereas pollen of *Xanthosoma* is always starchy and frequently trinucleate (see Grayum, 1985, 1986). In all of these respects, the two species described here are typical members of the genus *Chlorospatha.*

Chlorospatha croatiana Grayum, sp. nov. TYPE: Panama. Coclé: N slope and summit of Cerro Pilón, 900–1,173 m, *Croat 22932* (holotype, MO; isotypes B, K, PMA, US).

Planta terrestris; caulis erectus, subterraneus, saltem ad 22 cm longus; folia singulares paucive, lamina adulta 5–9-pedatisecta, glabra; petiolus (35–)50–70(–83) cm longus, purpureo-maculatus; lamina segmentum medium subaequilaterale, (17–)21–31(–43) cm longum, (6–)9–15(–20) cm latum, anguste ad late ellipticum; segmenta lateralia inaequilateralia. Inflorescentia ad usque 5–6; pedunculus 13–33(–48) cm longus, purpureus; spatha sub anthesi angusta, 7–9 cm longa; tubus (3–)4–6 cm longus, ad 7–9 cm longus in statu fructiferae, intus purpureus; spathae lamina alba, aliquanto cucullata; spadix 3.9–6.1 cm longa; pars feminea 1.2–2.4 cm longa, in dimidio inferiore spatha adnatae; pars sterilis 0.5–1.2 cm longa; pars mascula 2–2.7 cm longa; fructus albus; semina 15–25, alba, striata, ovoidea, 1–1.5 mm longa.

Terrestrial herb 0.5–2 m tall, the sap milky (e.g., *Churchill 3804*). Stems basally decumbent to erect, 5–22 cm or "sometimes ca. 1 m" (*Croat 22932*) long, 0.6–2.5 cm wide (dried), largely subterranean, clothed with weathered brownish and whitish cataphyll fibers. Leaves solitary or few, the petioles (35–)50–70(–83) cm long, terete, green and mottled with purple, at least toward the base, or else solid purple or purple-brown, vaginate in the lower one-fourth to one-half; lamina of adult leaf pedately 5–9-foliolate, glabrous, the central lobe more or less symmetrical, (17–)21–31(–43) cm long, narrowly to broadly elliptical, (6–)9–15(–20) cm broad, usually with 6–7 primary lateral veins per side. Lateral lobes progressively smaller than the central lobe, asymmetrical, the laminar tissue decurrent onto the upper side of the costae at base. Outermost lobes (second pair) acute to truncate, cordate or hastate at the base on the posterior side, only rarely (*Croat 49172*) differentiated basally into an additional (third) pair of lobes. Cataphylls lanceolate, 9–13(–20) cm long, drying reddish brown, persistent and becoming fibrous. Inflorescences up to 5–6, the peduncles 13–33(–48) cm long, purple. Spathe 7–9 cm long at anthesis, narrow, (4.5–)6–9 mm broad, slightly constricted centrally; spathe tube (3–)4–6 cm long at anthesis, green, purplish within, to 7–9 cm long in fruit; blade white to cream, curved forward and somewhat hooded, abscising soon after anthesis. Spadix 3.9–6.1 cm long, stipitate basally for 2.5–6

(–10) mm, the female portion 1.2–2.4 cm long, adnate to the spathe in the basal half (or apparently not at all in *Folsom 5870*); pistils more or less conical; sterile region 0.5–1.2 cm long, pink (*Dressler 4884*); staminodia all connate, the synandrodia drying pale with orange chromoplasts, subprismatic, flat-topped; male portion of the spadix 2–2.7 cm long, broadest at the base or toward the middle. Spadix (male portion?) variously reported as white or cream (*Hammel 3528, Dressler 4884, Knapp & Dressler 3471*) or purple (*Hammel 2571*). Fruits (in *Madison 775, Sytsma et al. 4244, Churchill 3804*) white, ca. 3–5 mm diam., 15–25-seeded. Seeds ovoid, white, longitudinally striate, 1–1.5 mm long, minutely brown-strophiolate. Pollen (pictured in Grayum, 1984) in planar tetrads, inaperturate, coarsely foveolate or reticulate, the individual grains 24–31 μm (mean 27 μm) diam., starchless, binucleate.

Distribution. *Chlorospatha croatiana* ranges from the Atlantic slope of central Costa Rica, southward throughout Panama and into northwestern Colombia.

The new species is named for Thomas B. Croat of the Missouri Botanical Garden, the foremost authority on Central American Araceae, one of whose ample collections has been selected as the holotype.

Chlorospatha croatiana can be divided at the outset into two subtaxa. Since these appear to be allopatric, they are here accorded the rank of subspecies.

Chlorospatha croatiana Grayum ssp. **croatiana.**
Figures 1, 2.

The "typical" subspecies is distinguished by its consistently 5-foliolate (very rarely 7-foliolate) leaves and Central American distribution.

Distribution. The first collection of ssp. *croatiana* was made in Limón Province, on the Atlantic slope of Costa Rica, in 1924 (*Standley 37356*). This remains the only known collection of the species from Costa Rica, and also represents the most northerly station for the genus as a whole. This sterile collection might be mistaken for *Xanthosoma pentaphyllum* (Vell.) Engl. (= *X. hoffmannii* Schott; see Bunting, 1979), which occurs on the Pacific slope of Costa Rica; the locality is suspicious, however, and the inclusion of the apical 2–3 cm of the clearly non-cormose caudex bearing the whitish and reddish brown cataphyll fibers characteristic of *C. croatiana* leaves little doubt as to the identity of the specimen.

This subspecies is most widely distributed in Panama. It is now known from every province except Herrera, Los Santos, and Veraguas—and will certainly turn up in the latter eventually. *C. croatiana* ssp. *croatiana* has been collected on wet slopes and along creeks, mostly in cloud forest, on either side of the continental divide, from 300 to 1,400 m (but mostly from 700 to 1,000 m). The Darién and Puerto Obaldía (San Blas) stations are so near the Colombian border that the subspecies will undoubtedly be found there sooner or later.

Flowering collections of ssp. *croatiana* have been made in all months except November, January, May, and September. The three known fruiting collections were made on 2 May and 22 and 26 October.

Chlorospatha croatiana ssp. *croatiana* is distinct from all other members of the genus except *C. gentryi* (described later in this paper) in its quinquefoliolate leaves. Only three other species of *Chlorospatha*—*C. kolbii, C. mirabilis* (M. T. Mast.) Madison and, the recently described, *C. corrugata* Bogner & Madison (Bogner, 1985)—are known to possess compound or essentially compound leaves. Both *C. kolbii* and *C. mirabilis* were briefly in cultivation during the late nineteenth and early twentieth centuries, and are believed to have originated from northern South America (see Madison, 1981). For the better part of the past hundred years, however, these species have been known collectively from just three herbarium specimens and a few illustrations (Madison, 1981). Though the possibility was considered that the Panamanian entity might represent one of these forgotten species, it does not agree well with the description of either (see Engler & Krause, 1920; Madison, 1981).

Chlorospatha kolbii differs from ssp. *croatiana* in its more numerous (seven to nine) and much shorter and narrower leaflets, supposedly scabrous above and with crispate-undulate margins, shorter and more slender petioles, shorter peduncles, and more prominently stipitate spadix with the female portion fully adnate to the spathe and the lower sterile flowers distinct.

Chlorospatha croatiana ssp. *croatiana* is more similar in overall dimensions to *C. mirabilis*. Two previously unidentified and uncited collections of the latter species were discovered and studied

during the course of the present investigation: *Killip 35091* (COL) and *Croat 56133* (COL), both from the Chocó region of Colombia. Living material of the latter collection is presently in cultivation at the Missouri Botanical Garden. Yet another recent Colombian collection is represented by living material at the Munich Botanical Garden and has been pictured by Bogner (1985). *Chlorospatha mirabilis* differs strikingly from *C. croatiana* in its trifoliolate, usually cream-spotted leaves and larger leaflets, frequently broadly confluent at the base.

The Colombian *Chlorospatha corrugata* is equally distinctive in its trifoliolate, deeply rugose laminae (see Bogner, 1985).

The available material of *C. croatiana* ssp. *croatiana* is somewhat variable, especially with respect to leaflet size and shape; but although occasional specimens appear distinctive in certain aspects (most notably *Hammel & Kress 13401*, from 300 m), a considerable range of this sort of variation is evident even within single populations (see especially *Luteyn & Kennedy 1804*). Thus I have little doubt that the collections listed hereunder all pertain to a single taxon.

Vegetatively, *C. croatiana* ssp. *croatiana* might be confused with some species of *Xanthosoma* with pedately compound leaves. The only one of these occurring in Panama is the widespread *X. helleborifolium* (Jacq.) Schott, which, unlike ssp. *croatiana*, is cormose and generally has narrower and more numerous (11–17) leaflets. Many species of *Syngonium* have pedately compound leaves, however all are scandent.

Specimens examined. COSTA RICA. LIMÓN: vicinity of Guápiles, *Standley 37356* (US).

PANAMA. BOCAS DEL TORO: Fortuna–Chiriquí Grande rd., 4.3 mi. N of Continental Divide, *Croat & Grayum 60208* (MO); 1.1 mi. W of Fortuna–Chiriquí Grande rd. near Continental Divide, *Croat & Grayum 60343* (MO). CHIRIQUÍ: Fortuna–Chiriquí Grande rd., 4.5–5 mi. N of dam, *Croat & Grayum 60078* (MO). COCLÉ: vicinity of Alto Calvario and near sawmill above El Copé, *Maas et al. 2740* (U), *Folsom 5870* (MO), *Hammel 2571, 3528* (MO), *Hammel & Kress 11329* (DUKE), *Croat 49172* (MO), *Knapp & Dressler 3471* (MO); N of El Valle de Antón, *Luteyn 3155* (DUKE); Cerro Pilón, *Croat 22932* (MO). COLÓN: headwaters of upper Río Piedras, *Sytsma et al. 4244* (MO). DARIÉN: Cerro Pirre, *Folsom 4340* (MO). PANAMÁ: Cerro Campana, *Bartlett & Lasser 16938* (MICH, MO), *Luteyn & Kennedy 1804* (DUKE), *Madison 775* (HUH), *Croat 22815* (MO); Río Pequení, 10–15 min. upstream from hydrographic station by motor, *Dressler 4884* (MO); between Tortí and Pilota del Toro, *Folsom et al. 5058* (MO); El Llano–Cartí Rd., *Hammel & Kress 13401* (DUKE); *Churchill 3804* (MO). SAN BLAS: forest SE of Puerto Obaldía, *Croat 16818* (SCZ); headwaters of Río Cangandi, *Hammel & de Nevers 13593* (MO).

Chlorospatha croatiana ssp. **enneaphylla** Grayum, ssp. nov. TYPE: Colombia. Boyacá: El Humbo, 130 mi. N of Bogotá, *Lawrance 794* (holotype, K).

A *Chlorospatha croatiana* ssp. *croatiana* lamina 7–9-pedatisecta differt.

A few Colombian collections exist of an entity that appears to be conspecific with *Chlorospatha croatiana*. Though agreeing with the Central American collections of ssp. *croatiana* in floral morphology and most vegetative characters, it differs consistently in having more leaflets. All three Colombian specimens with mature leaves are 7–9-foliolate, whereas only a single Central American specimen of the 23 examined exhibited even as many as seven leaflets. It seems appropriate, then, that the Colombian entity should receive taxonomic recognition.

Distribution. *Chlorospatha croatiana* ssp. *enneaphylla* is known only from northwestern Colombia, from the departments of Antioquia and Chocó and the western panhandle of Boyacá. Recorded elevations range from 350 to 600 m. The only dated flowering collection (*Shepherd 899*) is from 5 August.

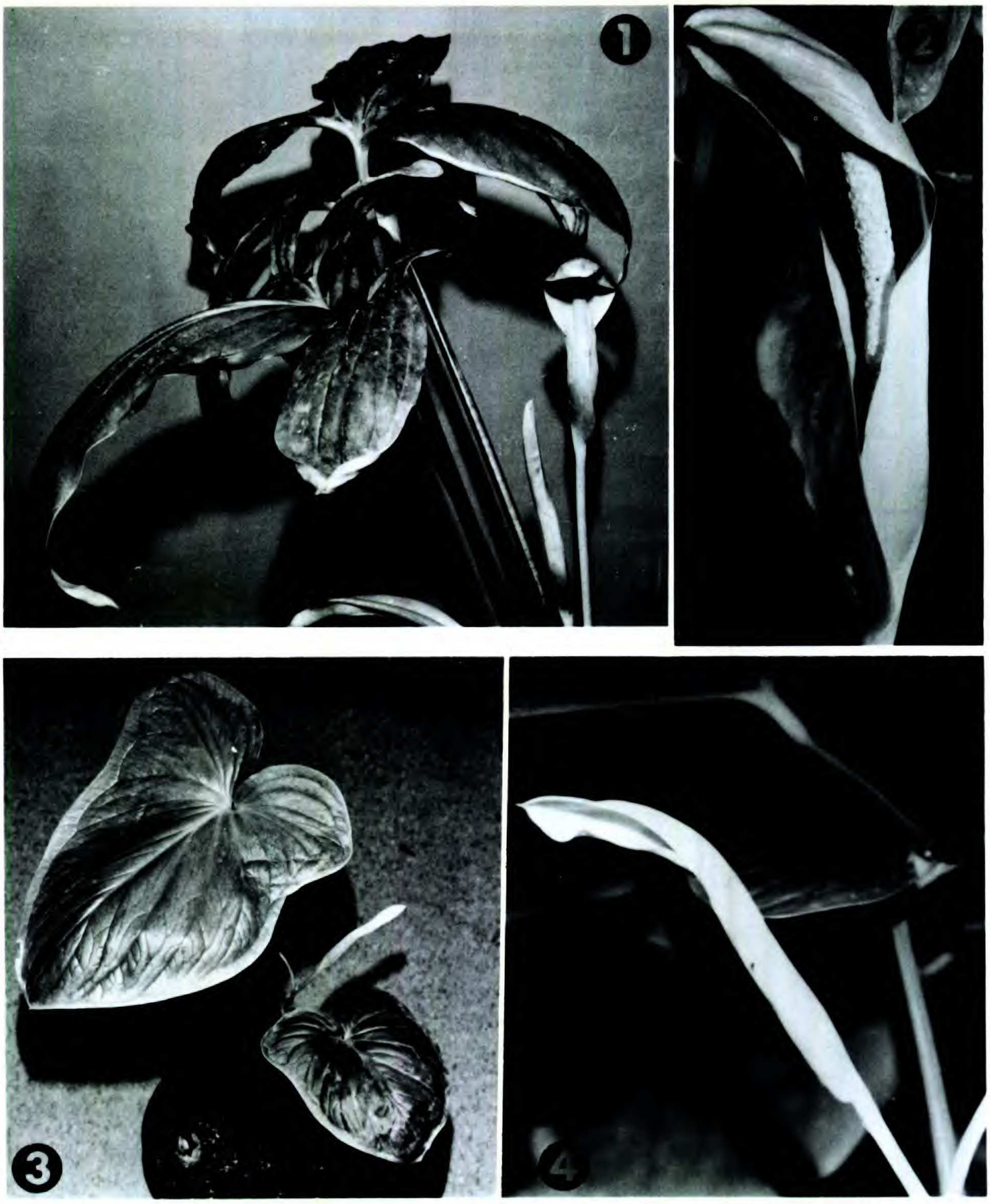
This taxon may be distinguished from vegetatively similar species of *Xanthosoma* inhabiting the region by its caulescent, rather than cormose, habit and its slender and delicate peduncles and inflorescences.

The two collections from Chocó are of sterile and presumably juvenile material; they are placed here speculatively, since they are atypical in leaf size and morphology.

Specimens examined. COLOMBIA. ANTIOQUIA: Río Anorí valley, *Shepherd 899* (WIS). BOYACÁ: El Humbo, *Lawrance 794* (K). CHOCÓ: between Medellín and Quibdó, *Croat 49311, 55930* (MO).

Chlorospatha hammeliana Grayum & Croat, sp. nov. TYPE: Panama. Coclé: just N of sawmill above El Copé, ca. 1,000 m, *Hammel & Kress 13465* (holotype, MO). Figures 3–6.

Planta terrestris; caulis saltem ad 8 cm longus; petiolus 40–65 cm longus, aliquanto spongiosus; lamina glabra, membranacea, simplex, ovata, basi profunde cordata vel sagittata; lobus anticus 23–35 cm longus, 16–27 cm latus; lobus posticus (9–)14–18 cm longus. Inflorescentiae 2–3; pedunculus 25–40 cm longus; spa-



FIGURES 1–4.—1, 2. *Chlorospatha croatiana* Grayum, sp. nov., ssp. *croatiana, Croat 22815.*—3, 4. *Chlorospatha hammeliana* Grayum & Croat, sp. nov., *Croat 44589* (this is a greenhouse-grown specimen; the leaves are disproportionately small as compared with wild-collected material). Photos by Thomas B. Croat.

tha angusta, 9–12 cm longa; tubus intus purpureus; spathae lamina alba vel subviridis; spadix 5.4–7.5 cm longa, pars feminea spathae adnatae ¼ to ⅓ longitudinis, 2.4–3.5 cm longa; pars sterili 1.4–2.2 cm longa; pars mascula alba, aliquanto clavata, 1.6–2 cm longa.

Terrestrial herb; stem appearing erect, 1–1.5 cm thick when dried, to at least 8 cm tall. Petioles 40–65 cm long, terete, somewhat spongy (i.e., easily compressible), glabrous, vaginate only in the basal one-sixth to one-fourth. Lamina of flowering individuals glabrous, simple, ovate, prominently cordate to sagittate basally, the anterior lobe 23–35 cm long, 16–27 cm broad, the posterior lobes (9–)14–18 cm long (measured along main vein). Lamina drying membranaceous and strongly bicolored (much paler below, with dark primary and secondary veins). Posterior costae denudate for 0.5–1.5 cm. Inflorescences 2–3, the peduncle 25–40 cm long. Spathe 9–12 cm long, narrow, constricted at summit of tube. Spathe tube greenish externally, purplish within; spathe blade white or greenish white, abscising after anthesis. Spadix 5.4–7.5 cm long; female portion 2.4–3.5 cm long, adnate to spadix

only in the basal one-fourth to one-third; female flowers pale, more or less conical, 2–2.2 mm long, with spreading, discoid style about the same diam. as the base of the ovary; stigmas yellowish; sterile part of spadix 1.4–2.2 cm long; synandrodia columnar or irregularly prismatic, 0.7–2.2 mm diam., more widely spaced than the fertile male flowers, whitish with reddish chromoplasts, the basal ones sometimes 4–6-lobed or divided. Fertile male region ca. 1.6–2 cm long, white, somewhat clavate; synandria prismatic, 4–5-thecate, truncate at apex, closely spaced. Pollen in planar tetrads, inaperturate, minutely rugulate or verruculate, the individual grains 23–25 μm (mean 24 μm) diam., starchless, binucleate.

Distribution. *Chlorospatha hammeliana* is known only from two isolated areas astride the Continental Divide in west-central Panama. At the type locality, near El Copé in Coclé Province, it occurs on steep slopes in very wet cloud forest on the Atlantic slope at 900–1,000 m. Two other sterile collections are from the area of Cerro Tute, near Santa Fe, Veraguas Province, at 700 m on the Atlantic slope and 1,050–1,150 m on the Pacific.

The single wild flowering collection (the holotype) was made on 25 August. (*Croat 44589* also includes fertile material, however the original wild collection was sterile; a live voucher flowered later in the greenhouse at the Missouri Botanical Garden—see Figs. 3–6—and was added to the collection.)

Chlorospatha hammeliana must be considerably rarer than *C. croatiana,* or perhaps it occurs in a more inaccessible habitat. Both species grow in the vicinity of the sawmill above El Copé, a popular collecting locality; but although *C. croatiana* seems to have been collected by virtually every botanist who has visited the site, *C. hammeliana* has been found but twice.

The new species is dedicated to Barry E. Hammel, now of the Missouri Botanical Garden, ardent and perspicacious collector and monographer of the flora of southern Central America, who first brought this plant to our attention.

Chlorospatha hammeliana is perhaps most similar to the Ecuadorian *C. besseae* Madison (1981; validated in Selbyana 7: 353. 1984, and again by Bogner, 1985), which likewise has simple, cordate leaves. That species, however, has shorter petioles and peduncles, smaller laminae, a smaller inflorescence, and orange male flowers. Furthermore, the female portion of the spadix in *C. besseae* is said to be completely adnate to the spathe.

Specimens examined. PANAMA. COCLÉ: N of sawmill above El Copé, *Croat 44589* (MO), *Hammel & Kress 13465* (MO). VERAGUAS: along trail to top of Cerro Tute, *Croat 48895* (MO); along Santa Fe–Calovébora rd., *Croat 48993* (MO).

During the course of the present investigation, yet another undescribed species of *Chlorospatha* was discovered among the collections of the Missouri Botanical Garden. This particularly distinctive species, from the Cordillera Occidental of northern Colombia, is described below. Though the male portion of the spadix (hence, the pollen) is unknown, the specimens conform in all other important respects to the most recent circumscription of *Chlorospatha* (Madison, 1981), to which the new species is therefore assigned without hesitation.

Chlorospatha gentryi Grayum, sp. nov. TYPE: Colombia. Antioquia: trail from Encarnación to Parque Nacional de los Orchídeas, W slope of Cordillera Occidental, 1,600–1,800 m, *Gentry & Rentería A. 24585* (holotype, MO-2715461; isotypes, COL, HUA). Figure 7.

Planta terrestris; caulis erectus saltem ad 10 cm longus; petiolus 12–20 cm longus, furfuraceus versus apicem; lamina 5-pedatisecta, secus venas venulasque subtus crispato-puberula, margine crispato-undulata; costa furfuracea; segmentum medium laminae aequilateralis, ellipticum, 6.5–9.5 cm longum, 3–4 cm latum; segmenta lateralia valde inaequilateralia. Inflorescentiae 2–3; pedunculus 6.5–9 cm longus, furfuraceus praesertim versus apicem; tubus spathae 2–2.5 cm longus, non nisi dorso extrinsecus dense furfuraceus, viridis, tenuibis longitudinalibus multinervis; spathae lamina alba; spadix pars feminea ca. 1.9 cm longa, sessilis, in dimidio inferiore spathae adnatae; spadix pars mascula ignota.

Terrestrial herb; stem erect, to at least 10 cm tall, 6–9 mm thick when dried. Petioles 12–20 cm long, slender, vaginate in basal one-fourth to one-third, clasping the stem, scurfy-pubescent with more or less flattened, branched, multicellular hairs in the apical one-half to one-fourth. Lamina pedately 5-foliolate, the margins crispate-undulate; lamina glabrous above, paler below and crispy-puberulent along the veins of all orders; costae naked or obscurely alate, with an indumentum like that of the upper petioles. Central lobe of lamina symmetrical or nearly so, elliptical, 6.5–9.5 cm long, 2.5–4 cm broad; lateral

FIGURES 5–7.—5, 6. *Chlorospatha hammeliana* Grayum & Croat, sp. nov., *Croat 44589*. Photos by Thomas B. Croat.—7. *Chlorospatha gentryi* Grayum, sp. nov., *Gentry & Rentería 24585* (Type). Photo by Alwyn H. Gentry.

lobes strongly asymmetrical, progressively smaller; all lobes acute at the base. Inflorescences 2–3, the peduncles 6.5–9 cm long, more or less densely crispy-puberulent especially in the apical part, the indumentum extending in a dense patch onto the dorsal surface of the spathe tube; spathe tube 2–2.5 cm long at anthesis, ca. 5 mm diam., greenish, finely longitudinally many-nerved; blade whitish, abscising soon after anthesis. Female part of spadix ca. 1.9 cm long, sessile (i.e., not stipitate), adnate to the spathe in the basal half. Male part of spadix unknown.

Distribution. To date, *Chlorospatha gentryi* is known only from the holotype, collected at 1,600–1,800 m on the western slope of the Cordillera Occidental in Antioquia Department, Colombia.

Chlorospatha gentryi, in its small, pedately-compound leaves with crispate-undulate margins, immediately recalls the elusive *C. kolbii.* It differs from that species, however, not only in its 5- rather than 7–9-pedatisect leaves, but also in its even shorter petioles and peduncles, non-stipitate spadix and crispy-puberulent indumentum (Engler & Krause, 1920, described the lamina of *C. kolbii* as "subholosericea," but only on the upper surface).

The new species is named for the collector of the holotype specimen, Alwyn H. Gentry of the Missouri Botanical Garden, one of the most active and authoritative field botanists working in the neotropics and a specialist on the flora of Pacific South America.

Specimens examined. COLOMBIA. ANTIOQUIA: trail from Encarnación to Parque Nacional de las Orchídeas, W slope of Cordillera Occidental, *Gentry & Rentería A. 24585* (MO, COL, HUA).

Inasmuch as the present paper significantly augments the number of compound-leaved *Chlorospatha* species known, a key to this assemblage is provided below:

KEY TO THE SPECIES OF *CHLOROSPATHA* WITH COMPOUND LEAVES

1a. Lamina trifoliolate, the leaflets narrowly to broadly confluent basally 2
  2a. Lamina deeply rugose, concolorous; lateral lobes nearly equaling median lobe; petiole less than 50 cm long ..... *C. corrugata* Bogner & Madison
  2b. Lamina relatively plane, frequently spotted with pale yellow or cream; median lobe nearly twice as long as lateral lobes; petiole more than 50 cm long ..... *C. mirabilis* (M. T. Mast.) Madison

1b. Lamina 5–9-foliolate, the leaflets narrowly confluent at the base or not at all 3
  3a. Lamina large, the central lobe more than 15 cm long and 5 cm broad; leaf margins plane; petioles more than 33 cm long 4
    4a. Lamina 5-(rarely 7-)pedatisect; southern Central America ..... *Chlorospatha croatiana* Grayum ssp. *croatiana*
    4b. Lamina 7–9-pedatisect; Colombia ..... *Chlorospatha croatiana* ssp. *enneaphylla* Grayum
  3b. Lamina small, the central lobe less than 15 cm long and 5 cm broad; leaf margins crispate-undulate; petioles less than 33 cm long 5
    5a. Lamina 5-pedatisect; petioles less than 25 cm long; peduncles less than 12 cm long; veins on lower side of leaf, costae, apical portions of petiole, peduncles and dorsal surface of spathe tube crispy-puberulent; spadix sessile ..... *Chlorospatha gentryi* Grayum
    5b. Lamina 7–9-pedatisect; petioles more than 25 cm long; peduncles more than 12 cm long; foliage not crispy-puberulent; spadix stipitate by 1.5 cm ..... *Chlorospatha kolbii* Engl.

With the addition of *Chlorospatha corrugata* Bogner & Madison and the three species just described to Madison's (1981) previous total of 11, the number of species now attributable to this suddenly burgeoning genus stands at 15. This represents nearly a fourfold increase in less than a decade (cf. Madison, 1978), occasioned by the installation of a clearly articulated generic circumscription coincident with the exploration of rich new habitats. Judging from the present rate of discovery and the number of intriguing sterile specimens filed away in herbaria, it seems likely that *Chlorospatha,* which lay dormant for nearly a hundred years, will eventually come to comprise as many as 20–25 species. The Chocó region of Colombia, which appears to be a stronghold of the genus, is one of the most botanically diverse and least-known areas remaining on the planet (Gentry, 1982), and can be expected to yield many interesting new species of Araceae. Perhaps it will also eventually yield additional material of the type species of *Chlorospatha, C. kolbii,* which, somewhat perplexingly, continues to elude rediscovery.

XANTHOSOMA

Over the past ten years, generic concepts in the tribe Caladieae have been arduously tested, mainly due to a major influx of specimens, comprising many new species, from the Andean re-

gions of Colombia, Ecuador, and Peru. *Chlorospatha*, not even recognized in its present circumscription a decade ago, has ironically emerged as perhaps the most distinctive of the three polytypic genera. It is well characterized by its caulescent habit, slender inflorescences with the female portion of the spadix usually fused with the spathe, widely spaced female flowers with thin, deliquescent, mantle-like styles dotted with red chromoplasts, oddly shaped synandrodia and small, starchless pollen borne in tetrads (Madison, 1981; Grayum, 1985).

The definitions of *Caladium* and *Xanthosoma* have, on the other hand, become more nebulous over the past ten years. In 1976, Michael Madison, who has made a specialty of this group and significantly clarified its taxonomy, published a list of six mainly vegetative and habital criteria that, he believed, could be used to distinguish *Caladium* from *Xanthosoma*. In all of these attributes—plant size (less than 0.5 m tall), habitat (not weedy), stem morphology (a globose tuber), peduncle length (relatively long), inflorescence number (solitary), and petiole attachment (peltate)—the species described below would fall more or less clearly into *Caladium*. In actual fact, however, several species of *Xanthosoma* were already known that violated one or more of these rules, and, in subsequent years, numerous additional aberrant species were described. The distinctions between the two genera finally became so blurred that, by 1981, Madison was forced to admit that "the single inflexible character separating them is the shedding of pollen in tetrads in *Xanthosoma* and in solitary grains in *Caladium*."

With the discovery of the following species, unique in violating all six of the above guidelines, the beleaguered generic concepts of *Xanthosoma* and *Caladium* have been subjected to their most formidable challenge yet—from which they emerge, I believe, unscathed, vindicated, and even reinforced.

Xanthosoma caladioides Grayum, sp. nov. TYPE: Panama. Comarca de San Blas, coast NE of Puerto Obaldía towards Colombian border, 8°40′N, 77°25′W, sea level, *Knapp & Mallet 4687* (holotype, MO-2982678). Figures 8, 9.

Planta terrestris vel epilithica, cormifera; petiolus 17–58 cm longus, ut videtur glaucus, laminae peltatim affixus; lamina glabra, membranacea, subtus glauca, simplex, ovata, basi cordata; lobus anticus 11–25 cm longus, 9–25 cm latus; lobus posticus 3.9–12.5 cm longus, rotundatus; distantia insertione petioli sinui laminae 2.7–5.5 cm. Inflorescentia solitaria; pedunculus (10.5–)12.5–33 cm longus; spatha sub anthesi 6.5–11 cm longa; tubus 2.5–5 cm longus, extus viridis, intus purpureus; spathae lamina (3.3–)4.3–6.3 cm longa, alba; spadix 5.3–9.8 cm longa, sessilis; pars feminea 1.6–2.9 cm longa, spathae vix adnatae; styli lati, discoidei, patuli; spadix pars sterili 1.4–2.7 cm longa, inferne dilatata, superne angustata; pars mascula 2.7–4.6 cm longa, 5–7 mm diametro, alba. Semina ca. 40–50, brunnea, tenuiter multicarinata, ovoidea, 0.8–1 mm longa. Pollinis granula quaternatim aggregatae.

Terrestrial or epipetric, acaulescent, cormose herb, ca. 25–50 cm tall. Corm subglobose, 1.5–2.5 cm diam. when dried. Leaves and "stems" (presumably petioles) glaucous (*Knapp & Mallet 4687*); petioles 17–58 cm long, vaginate in basal one-eighth to one-third, peltately attached. Lamina of adult leaf glabrous, drying membranaceous, glaucous below, apparently plain green above (*Allen 4629* appears to have darker markings, but the label is uninformative), simple and ovate, cordately lobed at the base, asymmetrically acute apically, the margins entire; anterior lobe (measured from insertion of petiole) 11–25 cm long, 9–25 cm broad, the posterior lobes (measured along main vein from insertion of petiole) 3.9–12.5 cm long, rounded; distance from petiole insertion to base of sinus 2.7–5.5 cm, the sinus more or less acute. Inflorescences 1 or 2 per plant, solitary in the sheaths, the peduncles (10.5–)12.5–33 cm long. Spathe 6.5–11 cm long at anthesis, constricted centrally; spathe tube 2.5–5 cm long at anthesis, ca. 1.4–2.3 cm broad when pressed, green externally, purple within, to ca. 6 cm long in fruit; blade (3.3–)4.3–6.3 cm long, white, abscising after anthesis. Spadix 5.3–9.8 cm long, slightly shorter than the spathe, sessile, the female portion 1.6–2.9 cm long, adnate to the spathe for 5 mm or less; pistils broadly conical, surmounted by a broad, spreading, discoid style, the ovary apparently with 3 partitions; sterile region of spadix 1.4–3.5 cm long, the basal third thicker than the female region, with the flowers bulbously enlarged, the apical two-thirds stipitate, narrower than the male region, the flowers vertically elongated and flattened; male portion of the spadix 2.7–4.6 cm long, widest in middle, ca. 4–7 mm broad when pressed, white; synandria flat-topped, roughly polygonal, with the margins sinuate, 0.5–2.2 mm in greatest diam., the anthers ca. 1.5 mm long and somewhat curved, dehiscing by apical pores. Fruits (in *Stern et al. 444*) ca. 3–3.3 mm diam. and whitish, when dried; seeds ca. 0.8–1 mm long, ovoid, brown, with 12–14 narrow, longitudinal keels; at least 45 counted in one intact fruit (*Bristan 1074*).

Distribution. *Xanthosoma caladioides* was first collected by Paul Allen in 1947 from Darién Province, Panama. It is still known from only eight collections, all from the Province of Darién and the Comarca of San Blas, in easternmost Panama. The three San Blas collections are all from near or at sea level, from near the Colombian border west to the vicinity of Playón Chico. Two of the Darién collections are from below 100 m in the valley of the Río Tuira, but *Allen 4629* was collected at 500–700 ft. on the inland slope of the Atlantic coastal range, and *Bristan 1074* appears to have come from the same general area. *Hammel 7314,* on the other hand, is from about 500 ft. in the remote Serranía del Sapo, fronting the Pacific coast. Thus, though little collected in this poorly explored end of Panama, *X. caladioides* is clearly widespread there. It certainly ranges into adjacent Colombia as well, at least along the Urabá coast, and perhaps into the Río Atrato basin, but no definite South American collections have been seen. A recent sterile collection (*Hammel 14162,* MO) of an unknown peltate-leaved aroid from primary forest on limestone at about 600 m in southwestern Costa Rica may also belong here.

Xanthosoma caladioides apparently may be either terrestrial or epipetric. The holotype, from San Blas, was collected in "tropical dry forest" with "strong sea winds"; the other two San Blas collections were from "coastal rocks . . . near the sea" (*D'Arcy 13692*) and in sandy soil, in deep shade in secondary growth (*Stier 34*). Two of the Darién collections were from along streambanks ("very common on steep, shaded banks," *Allen 4629*; "on slopes along stream," *Hammel 7314*), whereas *Stern et al. 444* was "growing on a vertical stone wall."

All of the recognizable collections of *Xanthosoma caladioides* are fertile, and all were made between 18 April and 30 June—the later collections representing mostly fruiting material. This period marks the onset of the rainy season in most of Panama (Foster, 1985). It is conceivable that *X. caladioides* passes much of the dry season in a leafless condition, as do several other species of the genus (pers. observ.).

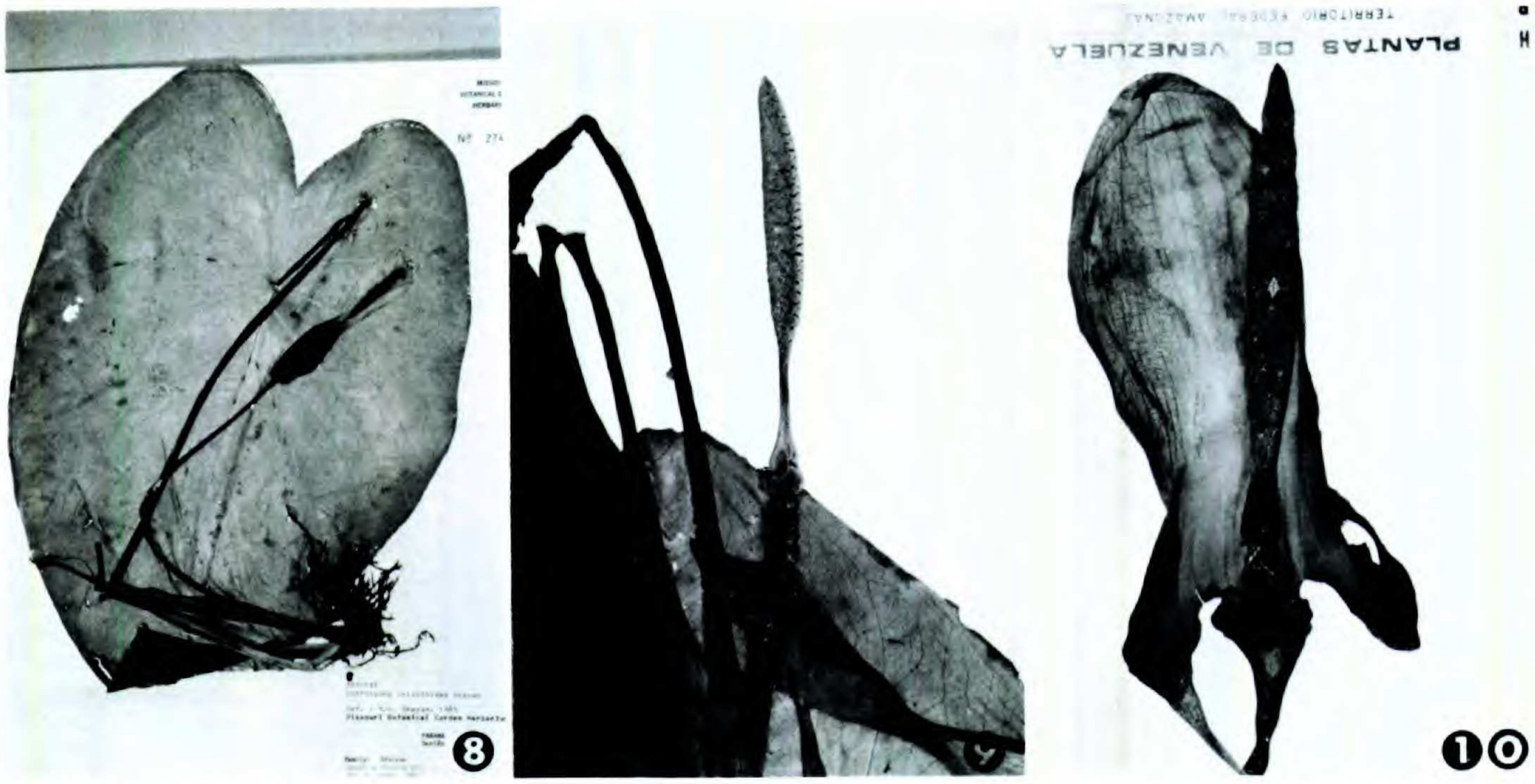
No information is available on pollination of *Xanthosoma caladioides.* I have noted that inflorescences at the anther-dehiscent stage (e.g., *Allen 4629, Stier 34*) tend to be lacking the enlarged basal sterile flowers, suggesting that these may serve as food-rewards for the pollinators (presumably dynastine scarab beetles).

Although one would not have anticipated the existence of any ethnobotanical information for such an obscure species, the label of *Stier 34* records the following: "kuidar [presumably a common name, in some unspecified indigenous language]—root used against fever."

The new species resembles the familiar, cultivated species *Caladium bicolor* (Ait.) Vent. so strikingly—at least on herbarium sheets—that it has been so determined repeatedly by several leading aroid specialists, including Madison himself. Vegetatively, the two species are virtually indistinguishable from dried material—though the posterior laminar lobes of *X. caladioides* are generally somewhat smaller and less divergent, and presumably the leaves are less frequently and/or less extensively variegated, if at all. (Regrettably, no plant of this species has ever been collected or, to my knowledge, even beheld alive by any aroid specialist, and none of the specimens is accompanied by fully adequate notes.) The resemblance also extends to the external aspect of the inflorescence.

Careful study of the inflorescence morphology, however, clearly reveals not only that the new species is not *Caladium bicolor,* but that it belongs unequivocally in the genus *Xanthosoma.* The first indication of this was provided by an examination of pollen under a compound light-microscope: pollen from all four polleniferous collections (*Stier 34, Allen 4629, Stern et al. 444, Hammel 7314*) was observed exclusively in tetrads. Two other technical, floral characters serve to distinguish *Caladium* and *Xanthosoma* in the vast majority of cases, and in both of these, the new species clearly agrees with the latter genus. First, broad, discoid, spreading styles, characteristic of *Xanthosoma* but lacking in *Caladium,* are plainly evident in the holotype specimen. Second, at least 45 seeds were counted in an intact fruit of *X. caladioides* (from *Bristan 1074*)—considerably above the maximum of 20 tolerated for *Caladium.* The multiovulate nature of *Xanthosoma* ovaries, incidentally, is probably closely correlated with the retention of pollen in permanent tetrads (Madison, 1981).

Two additional floral characters, though taxonomically insignificant at the generic level, may be of practical aid in distinguishing specimens of *Caladium bicolor* and *Xanthosoma caladioides*: the synandria of the former species are deeply notched marginally, whereas those of the latter are merely sinuate; and, the sterile region in *Caladium bicolor* is not so sharply differen-



FIGURES 8–10.—8, 9. *Xanthosoma caladioides* Grayum, sp. nov.—8. *Hammel 7314.*—9. *Knapp & Mallet 4687* (Type), inflorescence.—10. *Caladium bicolor* (Ait.) Vent., *Berry 640* (MO), Venezuela, inflorescence.

tiated into a narrowly stipitate apical portion and a bulbous basal portion, though there is a slight tendency in this regard (Figs. 9, 10).

Xanthosoma caladioides is not the first species of *Xanthosoma* known to have peltate leaves. The precedent was set a decade ago with the description of *X. peltatum* Bunting (1975) from Venezuela, about which the author later remarked: "el encuentro de esta especie andina cambia completamente nuestro concepto del género *Xanthosoma*" (Bunting, 1979). With our concept thus altered, the new species is neatly accommodated in *Xanthosoma.* It does not, however, appear closely related to *X. peltatum*—a much larger and coarser, arborescent plant of higher elevations—and one must suppose independent derivations of peltate leaves in these two species. The general aspect and inflorescence structure of *Xanthosoma caladioides* appear to ally it more closely with *X. mexicanum* Liebm. and related species, intractable violators of Madison's six criteria, from which it may be readily distinguished by its glabrous foliage, in addition to its peltate leaves.

Specimens examined. PANAMA. DARIÉN: Río Tuqueza below Québrada Venado, *Bristan 1074* (MO); headwaters of the Río Chico, *Allen 4629* (MO); Río Paya, near junction with Río Tuira (Boca de Paya), *Stern et al. 444* (MO); Río Pucuro, below village of Pucuro, *Duke 13141* (MO); Río San Antonio, upstream from Garachiné, *Hammel 7314* (MO). SAN BLAS: Playón Chico, Molia, *Stier 34* (MO); coastal rocks between Puerto Obaldía and Puerto Armila, *D'Arcy 13692* (MO); coast NE of Puerto Obaldía, *Knapp & Mallet 4687* (MO).

LITERATURE CITED

ANDRÉ, E. 1872. *Phyllotaenium lindeni.* Ill. Hort. 19: 3–5.

BOGNER, J. 1985. A new *Chlorospatha* species from Colombia. Aroideana 8: 48–54.

BUNTING, G. S. 1975. Nuevas especies para la revisión de las Araceas venezolanas. Acta Bot. Venez. 11: 263–335.

———. 1979. Sinopsis de las Araceae de Venezuela. Revista Fac. Agron. (Maracay) 10: 139–290.

CROAT, T. B. 1979. The distribution of Araceae. Pp. 291–308 *in* K. Larsen & T. B. Holm-Nielsen (editors), Tropical Botany. Academic Press, London.

ENGLER, A. & K. KRAUSE. 1920. Colocasioideae. Pp. 3–132 *in* A. Engler (editor), Das Pflanzenreich 71: (IV.23.E), W. Engelmann, Leipzig.

FOSTER, R. 1985. Plant seasonality in the forests of Panama. Pp. 255–262 *in* W. G. D'Arcy & M. D. Correa A. (editors), The Botany and National History of Panama: La Botánica e Historia Natural de Panamá. Monographs in Systematic Botany from the Missouri Botanical Garden, Volume 10.

GENTRY, A. H. 1982. Phytogeographic patterns as evidence for a Chocó refuge. Pp. 112–136 *in* G. T. Prance (editor), Biological Diversification in the Tropics. Columbia Univ. Press, New York.

GRAYUM, M. H. 1984. Palynology and Phylogeny of the Araceae. Unpubl. Ph.D. Thesis. Univ. of Massachusetts, Amherst.

———. 1985. Evolutionary and ecological significance of starch storage in pollen of the Araceae. Amer. J. Bot. 72: 1565–1577.

———. 1986. Phylogenetic implications of pollen nuclear number in the Araceae. Plant Syst. Evol. 151: 145–161.

MADISON, M. 1976. Luctatio aroideis I. *Caladium* and *Xanthosoma*. Phytologia 35: 103–107.

———. 1978. A synopsis of *Caladiopsis*. Contr. Gray Herb. 208: 95–98.

———. 1981. Notes on *Caladium* (Araceae) and its allies. Selbyana 5: 342–377.

NICOLSON, D. 1978. Araceae. Pp. 345–348 *in* A. C. Smith, A precursor to a new flora of Fiji. Allertonia 1: 331–414.

NOTE ADDED IN PROOF: *Chlorospatha croatiana* ssp. *croatiana* has recently been recollected in Costa Rica: HEREDIA: forest between Río Peje and Río Sardinalito, Atlantic slope of Volcán Barva, 10°17.5′N, 84°04.5′W, 700–750 m, *Grayum 6657* (MO).